

POLLINATION BIOLOGY OF *SILENE LEMMONII* (CARYOPHYLLACEAE),
A MONTANE PERENNIAL HERB

ALISA A. HOVE¹

Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA

ABSTRACT

Silene lemmonii S. Watson (Caryophyllaceae) is a tap-rooted herbaceous perennial that grows in montane habitats throughout California and Oregon. In 1999 and 2000, I studied the pollination biology and mating system of a single *S. lemmonii* population occurring near Dubakella Mountain in the Trinity National Forest, CA. Although *S. lemmonii* is self-compatible, individual flowers are strongly protandrous and fruit set rarely resulted from autogamy in both years of the study. *Silene lemmonii* flowers bloom at night, yet I observed no nocturnal insects visiting flowers in 1999 and visitation by diurnal bees and flies was infrequent during both years of the study. Despite the paucity of visitors, plants exhibited relatively high fruit set (\bar{x} = 40% in 1999 and \bar{x} = 61% in 2000). In 2000, I conducted an experiment to reconcile the occurrence of relatively high fruit set with rare insect visitation. I examined the contribution of insect visitation, autogamy, and jostling-induced geitonogamy (occurring when individual flowers on the same plant brush into one another) to fruit production. I found that fruit and seed production in *S. lemmonii* was primarily mediated by diurnal and nocturnal insect visits, but jostling-induced geitonogamy contributed to ~20% of fruit set. To my knowledge, this is the first study to report jostling-induced geitonogamy and the first to describe the pollination biology of *S. lemmonii*.

Key Words: Caryophyllaceae, geitonogamy, jostling-induced geitonogamy, nocturnal pollination, pollination, pollination syndrome, self-pollination, *Silene*.

The immobile nature of flowering plants makes most species dependent on animal pollinators to carry genetic material to and from potential mates. To attract pollinators, many flowering plants invest considerable resources in pollen and nectar production. However, visitation by animal pollinators can be erratic and unpredictable (Horvitz and Schemske 1990; Fenster and Dudash 2001; Price et al. 2005). Insufficient pollination caused by low visitation limits maternal reproductive success in many species (Burd 1994; Dudash and Fenster 1997; Ashman et al. 2004; Hampe 2005).

Two known alternatives to animal pollination include wind pollination (anemophily) and self-fertilization by autogamy (pollen transfer from anther to stigma within a single flower). Anemophilous flowering plants, such as grasses and oaks, possess several traits (e.g., unisexual, pendant flowers) that facilitate the transfer and receipt of pollen on wind currents (Proctor et al. 1996). While uncommon among species with flowers adapted to attract insect pollinators (entomophily), wind pollination can contribute to fruit production in entomophilous flowers occurring in windy areas (Gómez and Zamora 1996; Norman et al. 1997; Goodwillie 1999). Autogamy occurs in numerous self-compatible

taxa (Barrett 1998; Goodwillie et al. 2005), including many species in the genus *Silene* (Lesica 1993; Jürgens et al. 1996; Kephart et al. 1999; Buide and Guitian 2002; Keller and Schwaegerle 2006).

Geitonogamy (transfer of self-pollen between flowers on the same plant) caused by insects visiting multiple flowers on the same plant is well known (de Jong et al. 1993; Harder and Barrett 1995; Hodges 1995; Karron et al. 2004). However, another form of geitonogamous self-pollination –jostling-induced geitonogamy– may occur when self-compatible plants bear more than one flower. If wind causes adjacent flowers on the same plant to jostle into one another, pollen from one flower may move to another receptive stigma on the same plant.

The genus *Silene* (Caryophyllaceae) contains animal-pollinated species that vary in their pollination biology (e.g., Jürgens et al. 1996; Talavera et al. 1996; Brown and Kephart 1999; Buide 2006; Kephart et al. 2006). Several species possess red, day-blooming, hummingbird-pollinated flowers (Menges 1995; Fenster et al. 2006), whereas others have pale, night-blooming flowers that are pollinated by noctuid or sphingid moths (Pettersson 1991; Young 2002; Barthelmess et al. 2006; Kephart et al. 2006). *Silene lemmonii* S. Watson is a pale-flowered, night-blooming species whose pollination biology was relatively unknown prior to this study.

The objectives of this investigation were to study the pollination biology of *S. lemmonii*,

¹Current Address: Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, email: hove@lifesci.ucsb.edu

determine the relative importance of diurnal and nocturnal pollination, and evaluate the relative importance of biotic and abiotic pollination. *Silene lemmonii* has protandrous flowers, wherein each flower appears to shed pollen prior to stigma receptivity. Preliminary observations revealed that insect visits to *S. lemmonii* occurred during the day, while its petals were withered. Furthermore, insect visitation appeared uncommon, yet fruit set seemed relatively high. Since even slight breezes can blow *S. lemmonii*'s glandular-hairy inflorescences into one another (A. Hove, *personal observation*) and flowers in the male and female phases of development frequently occur in close proximity on the same plant, I hypothesized that jostling-induced geitonogamy could contribute to fruit production.

In 1999 and 2000, I conducted a series of observational and experimental studies to address the following questions: (1) Which insect taxa visit *S. lemmonii*?; (2) What fraction of insect pollination occurs during daylight hours compared to twilight and evening hours?; (3) What is the timing of the male (pollen-shedding) phase relative to the female (stigma-receptive) phase within individual flowers?; (4) Is *S. lemmonii* self-compatible? If so, does autogamy occur under natural conditions?; and, (5) During the 2000 flowering season, to what extent does jostling-induced geitonogamy contribute to fruit set and seed set?

METHODS

Study Species

Silene lemmonii is a tap-rooted herbaceous perennial found in oak woodlands and coniferous forests of mountain ranges in southern Oregon (Kozloff 2005) and throughout California, including the Klamath Range, Santa Cruz Mountains, Sierra Nevada Range, and Transverse Ranges (Hickman 1993). The vegetative plant body has low-growing stems and its growth form ranges from creeping to erect. When in flower, plants appear much taller (between 40–70 cm), displaying pendant flowers arranged in cymose inflorescences with elongate rachises (Fig. 1). The inflorescence rachises remain smooth while flowers are in bud and then become sticky with glandular hairs as the flowers begin to open. During the flowering season, adjacent inflorescence rachises on an individual plant sometimes stick to one another (A. Hove, *personal observation*).

In 1999, each plant bore an average of 8.2 inflorescences ($n = 130$ plants), which displayed two to four open flowers throughout the flowering season (A. Hove, unpublished data). Thus, the average number of open flowers per plant at a given time during the flowering season typically

ranged from approximately 16 to 32. Plants varied greatly in flower production, with small plants bearing one flower and the largest plants bearing nearly 70 flowers. On average however, individuals produced 20.5 flowers per plant ($n = 70$, $SE = 1.97$) during a flowering season.

Silene lemmonii flowers have no detectable fragrance and produce little to no nectar (A. Hove, unpublished data). The yellowish-white to pale pink petals wither during the heat of mid-day and then unfold at dusk, remaining expanded into the evening and early morning hours. Stigmas appear receptive and anthers display copious amounts of pollen during both the daylight and evening hours.

Study Site

In 1999 and 2000, I studied a large population of *S. lemmonii* growing near Dubakella Mountain in Trinity County, California. The site is located in the Trinity National Forest approximately 32 km southeast of Hayfork. At the site, *S. lemmonii* was abundant in the herbaceous understory within the mixed coniferous forest. The flowering season began in late May–early June and ended in early July. Wind speeds recorded during the 2000 flowering season did not exceed 8 kph ($\bar{x} = 0.97$ kph, $SE = 0.12$).

Identification of Floral Visitors and Their Visitation Rates

To identify insect visitors, determine their corresponding visitation rates, and ultimately estimate the number of visits a flower receives during its lifetime, I established four observation stations in 1999 and five stations in 2000. I placed the observation stations at least 150 m apart from one another at various locations in the population. At each station, I tagged all plants whose flowers could be easily monitored without the aid of binoculars by an observer sitting approximately 1.5 m away from the plants.

Field workers conducted hour-long observations throughout both flowering seasons during the following time periods: morning (sunrise–1200), afternoon (1200–1800), twilight (1800–2100), and night (2100–sunrise). For night observations, two people worked together, using red lights to view floral visitors. In 2000, field workers recorded wind speed with an anemometer approximately every 20 min for the duration of each observation period.

When insects visited flowers, field workers recorded visitor identity, number of flowers visited, the gender-phase of each flower visited, and whether the insect foraged on nectar or pollen. Visitors were captured for identification if possible. I observed 26 plants for a total of 16 hrs in 1999 and 57 plants for a total of 20 hrs



FIG. 1. Drawing of a *Silene lemmonii* plant. Copyright provided by the artist, Alex Yelich.

in 2000. Observation periods were distributed evenly across plants during both years of the study.

Visitation rates (# insect visits flower⁻¹ hr⁻¹) were calculated for each visiting insect taxon. Because of infrequent insect visitation in 1999 and 2000, I also calculated a pooled visitation rate (# visits by all insect taxa flower⁻¹ hr⁻¹) for each year. I estimated the number of open flowers per plant by multiplying the mean number of inflorescences per plant and the mean number of open flowers per inflorescence (n = 130 plants).

In both years, I estimated the total number of visits a flower receives over its lifetime as the product of the pooled visitation rate and the average number of hours a flower stays in bloom (216 hrs in 1999 and 118 hrs in 2000). My estimates of total visit number depend on several

parameters, most of which are themselves estimates: the number of inflorescences per plant, the number of flowers per inflorescence, and floral lifespan. To evaluate the sensitivity of calculated visitation rates and expected floral visits to changes in estimated parameters, I conducted two sensitivity analyses by varying the magnitudes of two of these parameters (number of open flowers per plant and floral lifespan) and examining the subsequent effect of each of these changes on the pooled visitation rate and expected visit number per flower.

Comparison of Diurnal versus Nocturnal
Insect Pollination

During both field seasons I conducted an experiment designed to evaluate the relative

contribution of diurnal and nocturnal insect pollination to fruit and seed production. I used cages made of window-screening mesh (with 1.4 mm \times 1.6 mm openings) to exclude pollination by either diurnal or nocturnal visitors. I assigned each plant in this experiment to one of the following three treatments: *i.* caged from sunrise to sunset and exposed to potential pollinators during the twilight and nighttime hours (hereafter referred to as "night"); *ii.* caged from sunset to sunrise and exposed during the day; or *iii.* uncaged and exposed to potential diurnal and nocturnal pollinators for the entire flowering season. The uncaged plants served as a control group, allowing me to assess the total amount of fruit and seed production resulting from both diurnal and nocturnal pollination.

In 1999, I randomly selected 105 plants throughout the population. I made 20 plants available only to nocturnal pollinators and I made 20 plants available only to diurnal pollinators. Sixty-five control-group plants remained uncaged and accessible to both diurnal and nocturnal pollinators throughout the flowering season. In 2000, I randomly selected 120 plants from the population. I caged 40 plants at night, leaving them exposed during the day. I also caged 40 plants during the day and exposed them at night. I assigned 40 plants to the control group.

At the end of both field seasons, I collected all mature fruits on the plants, stored them individually in coin envelopes, and dried them at 110°C for four days. Fruits typically contained seeds that appeared viable (hereafter referred to as "viable"), filled ovules, and unfertilized ovules, all of which were visually distinguished from one another with a dissecting microscope (*sensu* Kephart et al. 1999). Large and plump seeds, with furrowed reddish-brown seed coats, were considered viable. Filled ovules were smaller than viable seeds, flattened, and lacked well-developed seed coats. Both viable seeds and filled ovules were easily distinguishable from the much smaller and flatter, presumably unfertilized ovules. In 1999 and 2000, I assessed seed set by counting the number of viable seeds per fruit.

In 1999 and 2000, I compared mean fruit set (number of fruits produced/total number of flowers per plant) among the three treatment groups with one-way ANOVAs followed by Fisher's LSD Multiple Comparison Tests. I also used one-way ANOVAs and Fisher's LSD Multiple Comparison Tests to compare mean seed set among the three groups for both years of the study. I removed 45 plants in 1999 and 47 plants in 2000 from the analysis because of mortality resulting from either anther smut disease or herbivory (to evaluate the distribution of these removals across treatments, refer to actual sample sizes presented in Table 3).

Timing of the Male and Female Phases of Floral Development

In 1999 and 2000, I randomly selected plants from the population and daily monitored four flowers per plant. I observed 15 plants in 1999 ($n = 60$ flowers) and 10 plants ($n = 40$ flowers) in 2000. For each flower, I noted the duration of its male phase as well as its female phase. I considered flowers to be male once anthers began to release fresh pollen until all the anthers withered. The female phase commenced when stigmas appeared moist and papillate, lasting until the styles began to wither. In 1999, I conducted hydrogen peroxide tests (Kearns and Inouye 1993) on 20 moist-papillate stigmas to confirm their receptivity and my ability to visually identify a flower's female phase.

Degree of Self-compatibility and Capacity for Autogamy

To determine *S. lemmonii*'s degree of self-compatibility, I randomly selected and caged 20 plants in 1999 and 40 plants in 2000. To prevent pollination by visiting insects and browsing by deer, plants remained caged until fruit maturation occurred.

I randomly assigned 15 female-phase flowers on each plant to one of three possible hand-pollination treatments: *i.* addition of self-pollen (pollen from a male-phase flower on the same plant); *ii.* addition of pollen from two distant plants; or *iii.* unmanipulated (no supplemental pollen provided). Each treatment group typically contained five flowers. Hand-pollinations involved brushing freshly dehiscent anthers against receptive stigmas to cover them with pollen grains.

In 1999, flowers from treatment group *iii* failed to produce fruits, so I used paired two-tailed *t*-tests to compare mean fruit set and mean seed set between treatment groups *i* and *ii*. In 2000, I compared mean fruit set among treatment groups *i*, *ii*, and *iii* using two-way ANOVAs (with treatment as the main effect and plant as a block effect) followed by Tukey's HSD Multiple Comparison Tests. I compared mean seed set among the three groups using a nested ANOVA with treatment nested within plant. Four plants in 1999 and 16 plants in 2000 were excluded from the analysis due to either anther smut disease or inability to replicate all three experimental treatments on a single plant.

Determining the Importance of Biotic versus Abiotic Pollination

In 2000, I conducted an experiment to assess the relative contribution to fruit and seed set made by autogamy, insect visitation, and jostling-

TABLE 1. RELEVANT COMPARISONS AND THEIR IMPLICATIONS FOR THE EXPERIMENT DESIGNED TO DETERMINE THE RELATIVE IMPORTANCE OF ABIOTIC VERSUS BIOTIC SOURCES OF POLLEN IN 2000. Pollen sources available to plants included in each treatment group (caged, emasculated, pruned, or unmanipulated) are included in parentheses (a = autogamy, i = insect visitation, and j = jostling-induced geitonogamy). See also caveats described in the Results and Discussion sections.

Implications of Pairwise Treatment Comparisons
— If fruit/seed set of unmanipulated plants (a, i, j) > pruned plants (a, i), then jostling contributes pollen (provided that visitation rates to pruned and unmanipulated plants are similar and pruning does not reduce a plant's attractiveness to pollinators).
— If fruit/seed set of unmanipulated plants (a, i, j) = emasculated plants (i), then insect visitation and/or autogamy contributes pollen and jostling-induced geitonogamy does not contribute pollen.
— If fruit/seed set of pruned plants (a, i) > emasculated plants (i), then autogamy contributes pollen.
— If fruit/seed set of unmanipulated plants (a, i, j) > caged plants (a, j), then insect visitation contributes pollen.

induced geitonogamy. I randomly selected and assigned 160 plants to one of the following four treatment groups: *i.* caged for the duration of its flowering; *ii.* emasculated (removal of all anthers on the plant); *iii.* pruned (selective removal of inflorescences to prevent flowers from contacting others on the same plant or neighboring plants); or *iv.* unmanipulated (all inflorescences and anthers left intact). Each treatment group contained 40 plants. Pruned plants retained three to five inflorescences.

By differing in available sources of pollen, each experimental treatment group provided an insight regarding the importance of different pollination sources to reproduction (Table 1). Yet it should be noted that by imposing these treatments, I potentially introduced the additional sources of variation (also see Discussion section) described below. For example, caging plants provided a measure of maternal reproductive success in the absence of insect visitors. However, cages also sheltered plants from slight breezes and the window-screening mesh may have provided a surface to which sticky inflorescences could adhere; this potentially reduced, but could not eliminate inflorescence jostling within a plant. By emasculating plants, I could evaluate the contribution of insect visitation by itself to fruit and seed production. Pruning inflorescences ruled out jostling-induced geitonogamy, but autogamy and insect visitation remained as potential means of pollination. However, emasculated plants may have been less attractive to pollen-foraging insects and pruned plants (with their reduced floral displays) may have been less attractive to insects in general. The unmanipulated plants provided an overall estimate of maternal reproductive success attributable to all three possible pollination sources.

I compared mean fruit set, as well as mean seed set, among the treatment groups using one-way ANOVAs followed by Fisher's LSD Multiple Comparison Tests. By comparing pairs of treatments differing by just one source of pollen, I

could estimate the importance of each pollen source to fruit and seed set (Table 1). For example, I predicted that if jostling contributed pollen, then unmanipulated plants (all three sources of pollen possible) would have higher fruit and seed set than pruned plants (only autogamy and insect-borne sources of pollen possible). I removed 48 plants from the analysis because of either herbivory or anther smut disease (to evaluate the distribution of these removals across treatments, refer to actual sample sizes presented in Table 6).

RESULTS

Identities of Floral Visitors and Visitation Rates

During both years, I recorded a total of at least seven taxa of visiting insects (Table 2). Flies (Diptera) and moths (Lepidoptera) made the majority of visits. Bees (Hymenoptera) also visited the flowers, but were much less common (Table 2). I observed an additional seven visits by small flies that could not be caught for identification.

The identities of insect visitors varied between 1999 and 2000. Even though *S. lemmonii*'s pale petals are most conspicuous at night, I observed no nocturnal visits during six hours of twilight and nocturnal observation in 1999. Instead, pollen-foraging syrphid flies (Syrphidae) visited most often in that year (Table 2). In 2000, on the other hand, nectar-foraging moths (Noctuidae) were the most frequent floral visitors with eight visits recorded over 11 hrs of twilight and nocturnal observation. Diurnal bees and flies also visited plants during the day in 2000. In both years, yellow-headed bumblebees (*Bombus vosnesenskii*) rarely visited (Table 2), but were abundant at the site, commonly foraging on neighboring snowberry (*Symphoricarpos mollis*) and lupin (*Lupinus latifolius*) flowers.

Insect visitation was infrequent in both 1999 and 2000. I recorded 26 insect visits over 16 hrs

TABLE 2. INSECT VISITORS TO *SILENE LEMMONII* OBSERVED IN 1999 AND 2000 AND THEIR ESTIMATED VISITATION RATES. Visitation rates were calculated based on the average number of open flowers per plant (24.56). Twenty-six plants were observed for 16 hrs (10 daylight hrs, 6 twilight or night hrs) in 1999 and 57 plants were observed for 20 hrs (9 daylight hrs, 11 twilight or night hrs) in 2000. The pooled visitation rate (visitation rate pooled for all insect taxa in a year) was 2.54×10^{-3} visits flower⁻¹ hr⁻¹ in 1999 and 7.86×10^{-4} visits flower⁻¹ hr⁻¹ in 2000. Unknown flies were observed visiting, but could not be caught for identification.

Year	Insect Taxon (Order)	Number of Observed Visits	Visitation Rate (# visits flower ⁻¹ hr ⁻¹)
1999	<i>Bombus vosnesenskii</i> (Hymenoptera)	1	9.8×10^{-5}
	Syrphidae (Diptera)	16	1.6×10^{-3}
	Megachilidae (Hymenoptera)	4	3.9×10^{-4}
	Unknown Fly (Diptera)	5	4.9×10^{-4}
2000	<i>Bombus vosnesenskii</i> (Hymenoptera)	1	3.6×10^{-5}
	Noctuidae (Lepidoptera)	8	2.9×10^{-4}
	Syrphidae (Diptera)	6	2.1×10^{-4}
	Megachilidae (Hymenoptera)	3	1.1×10^{-4}
	<i>Osmia</i> sp. (Hymenoptera)	1	3.6×10^{-5}
	Bombyliidae (Diptera)	1	3.6×10^{-5}
	Unknown Fly (Diptera)	2	7.1×10^{-5}

of observation in 1999 and 22 visits over 20 hrs of observation in 2000. Consequently, taxon-specific visitation rates calculated for each visitor taxon were extremely low in both years of the study (Table 2), as were visitation rates pooled across all insect taxa. The visitation rate pooled across all insect taxa was 2.54×10^{-3} visits flower⁻¹ hr⁻¹ in 1999 and 7.86×10^{-4} visits flower⁻¹ hr⁻¹ in 2000, based on an estimated average number of 24.56 open flowers per plant. I predicted that an individual flower had little chance of receiving a single visit during its lifetime for both years of this study. Based on the pooled visitation rates estimated for the study population, a single flower could expect to receive 0.55 visit in 1999 and 0.09 visit in 2000.

Both of the sensitivity analyses I conducted indicated that both visitation rate and the expected visit number over the floral lifetime remain low even when I vary the estimates of average number of open flowers and the duration of the floral lifespan (Fig. 2). I examined the impact of varying flower number on calculated visit rates because I was concerned that my estimate of the average number of open flowers per plant may have been too high. However, even when I reduce average the number of open flowers per plant to 10, calculated rates remain very low (6.25×10^{-3} in 1999 and 1.93×10^{-3} in 2000). Additionally, the total number of insect visits over a flower's lifetime is likely an overestimate because insects were not active for all 120 hrs of a flower's lifetime. For instance, I never observed insect visitors in the early morning (0100–0300), but flowers stayed open during those hours. A flower's probability of receiving a visit decreases if I account for the number of hours insects may be available. If, for example, insects visit flowers for only 100 hr of

the floral lifetime, a single flower could expect 0.25 visit in 1999 and 0.08 visit in 2000.

Proportion of Pollination Occurring During Daytime versus Evening Hours

During both field seasons, caging plants for some portion of a 24-hour period decreased fruit production. In 1999, flowers accessible to visitors throughout the day and night produced more fruits than did flowers exposed only during the day (Table 3). Fruit set among night-exposed plants did not statistically differ from that of plants exposed during the day or that of uncaged plants (Table 3). Mean seed set did not differ among the three treatment groups in 1999 (Table 3).

In 2000, uncaged plants exhibited significantly greater fruit set and seed set than those exposed solely during the day or night (Table 3). Unlike the previous year, night-exposed plants in 2000 had greater fruit set and seed set than day-exposed plants (Table 3). Excluding visitors during either the day or night also reduced seed production in 2000. However, night-exposed plants had greater seed set than those exposed during the day (Table 3).

Timing of Male and Female Phases of Floral Development

Silene lemmonii flowers are strongly protandrous with very little overlap of their male and female phases; filaments are extended and anthers shed pollen prior to stigma receptivity. In 1999, the male phase lasted for average of 2.7 d (SE = 0.55) and the female phase lasted for an average of 6.4 d (SE = 0.86). In 2000, the male phase lasted for an average of 2.79 d (SE = 0.15) and

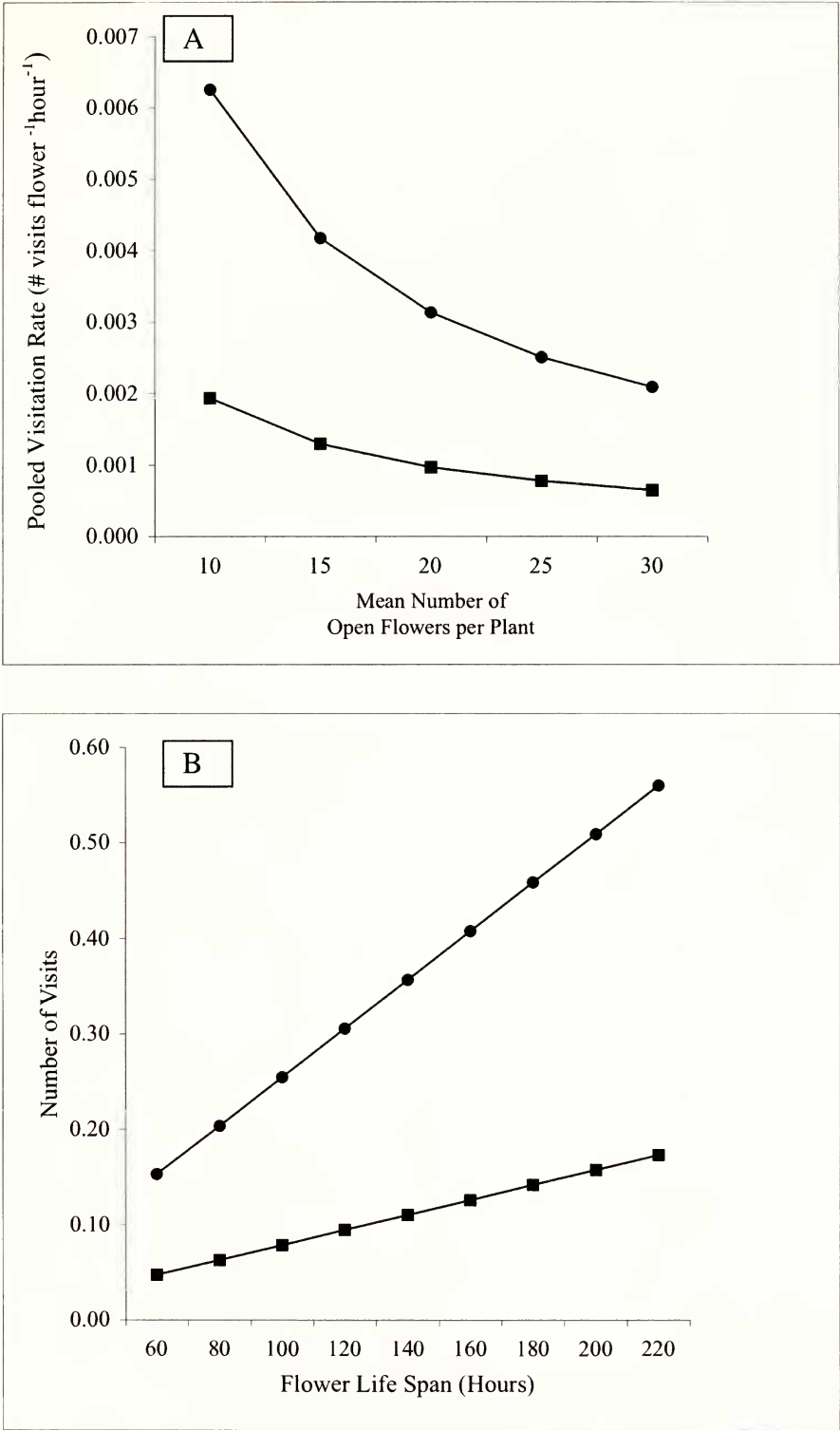


FIG. 2. Results of sensitivity analyses evaluating; A. the effect of varying average flower number on the estimation of the pooled insect visitation rate; and B. the effect of varying flower life span on the estimated number of visits a flower receives over its lifetime. Estimation of visit number is based on the average number of open flowers per plant (24.56). Circles (●) indicate results from 1999; squares (■) indicate results from 2000.

TABLE 3. COMPARISON OF MEAN FRUIT AND SEED SET OF PLANTS THAT WERE UNCAGED, EXPOSED ONLY DURING THE DAY, OR EXPOSED ONLY AT NIGHT IN 1999 AND 2000. For each year means with identical superscripts are not significantly different (Fisher's LSD Multiple Comparison Test, $P < 0.05$). N = the number of plants per treatment. For some treatments, seed set N < fruit set N because Lepidoptera larvae consumed all the seeds produced by a plant. NS = not significant, * = $P < 0.05$, ** = $P < 0.005$.

Year	Treatment	Mean Fruit Set (SE)	N	F-ratio	Mean Seed Set (SE)	N	F-ratio
1999	Day open	0.09 (0.035) ^a	7	4.51*	6.15 (0.64) ^a	6	0.69 ^{NS}
	Night open	0.17 (0.065) ^{ab}	7	df = 2, 57	6.88 (1.23) ^a	5	df = 2, 61
	Day and night open	0.40 (0.049) ^b	46		6.78 (0.96) ^a	20	
2000	Day open	0.23 (0.031) ^a	19	34.57**	6.89 (0.58) ^a	18	54.43**
	Night open	0.34 (0.037) ^b	24	df = 2, 70	9.22 (0.43) ^b	22	df = 2, 606
	Day and night open	0.61 (0.032) ^c	30		12.71 (0.26) ^c	30	

the female phase lasted for an average of 2.11 d (SE = 0.16).

Self-compatibility

Silene lemmonii appears to be fully self-compatible. Fruit set and seed set of self-pollinated flowers matched that of outcrossed flowers in both years of the study. In 2000, both treatment groups had greater fruit set than in the previous year (Tables 4 and 5). Additionally, flowers appear to have little capacity for autogamy. In 1999, none of the caged, unmanipulated flowers produced fruits. In 2000, approximately 12% of the caged, unmanipulated flowers produced fruits, but seed set of these fruits was low compared to that of self-pollinated and outcrossed fruits (Tables 4 and 5).

Effects of Pruning, Caging, or Emasculating Flowers on Fruit Set and Seed Set

Mean fruit set differed among the four experimental treatment groups (one-way ANOVA, $F_{3,108} = 35.02$, $P < 0.001$; Table 6). On average, approximately 61% of flowers on unmanipulated plants set fruit, exhibiting greater fruit set than plants from the other three treatment groups (Table 6). In contrast, caged plants set significantly fewer fruits (~10%) than the other three groups. Fruit set experienced by

pruned plants (~46%) did not differ statistically from that of emasculated plants (~49%) (Table 6).

Seed set varied among the four treatment groups (Table 6). However, the differences in seed set among the groups did not directly correspond with the differences found in fruit set, and average seed set differed statistically among all four treatment groups. Pruned plants had the greatest seed set, followed by unmanipulated plants, emasculated plants, and then caged plants (one-way ANOVA, $F_{3, 726} = 65.83$, $P < 0.0001$; Table 6).

DISCUSSION

For many years, the level of specialization versus generalization characterizing plant-pollinator interactions has been the subject of robust debate (Waser et al. 1996; Johnson and Steiner 2000; Gómez 2002). Pollination syndromes, or the presence of highly specific suites of floral traits that attract particular pollinators or facilitate a specialized type of pollination (Procter et al. 1996), are an intuitive and appealing way to both explain the large diversity of both flowering plants and pollinating animals and to gain a preliminary understanding of plant-animal coevolutionary processes. However, numerous studies indicate that flowering plants receive pollination services from many different animal

TABLE 4. COMPARISON OF MEAN FRUIT AND SEED SET BY SELF-POLLINATED, OUTCROSSED, AND UNMANIPULATED CAGED FLOWERS IN 1999 AND 2000. For each year means with the same superscripts are not significantly different (Paired t-test or Tukey's HSD Multiple Comparison Test, $P < 0.05$). N = the number of plants per treatment. NS = not significant, * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.0005$.

Year	Treatment	Mean Fruit Set (SE)	N	Test statistic	Mean Seed Set (SE)	N	Test statistic
1999	Self-pollinated	0.42 (0.11) ^a	16	t = 0.58 ^{NS}	5.41 (1.29) ^a	8	t = 0.78 ^{NS}
	Outcrossed	0.33 (0.096) ^a	16		7.00 (1.60) ^a	9	
	Unmanipulated	0	16				
2000	Self-pollinated	0.55 (0.063) ^a	24	F = 4.75***	10.93 (0.94) ^a	24	F-ratio = 2.55***
	Outcrossed	0.61 (0.065) ^a	24		12.65 (0.84) ^a	24	
	Unmanipulated	0.12 (0.052) ^b	24		4.40 (1.97) ^b	24	

TABLE 5. The EFFECTS OF POLLINATION TREATMENT (SELF, OUTCROSS, AND CONTROL) AND MATERNAL PLANT ON FRUIT SET AND SEED SET IN 2000. Fruit set was compared with a two-way ANOVA, with plant as a block effect. Seed set was compared using a nested ANOVA, with treatment nested within plant.

Fruit Set				
	df	SS	F-ratio	P
Model	25	6.79	4.75	<0.0001
Plant	23	3.34	2.53	0.0036
Treatment	2	3.45	30.17	<0.0001
Error	46	2.63		

Seed Set				
Model	50	3221.18	2.55	0.0003
Treatment	2	533.52	10.57	0.0001
Treatment (plant)	48	2639.3	2.18	0.0024
Error	58	4685.56		

taxa (Stephenson and Thomas 1977; Herrera 2005; Buide 2006). Furthermore, pollinator abundances can vary over space and time (Moeller 2005; Price et al. 2005). This spatiotemporal variation in pollination service is one factor thought to promote self-fertilization in plant species (Kalisz and Vogler 2003; Morgan and Wilson 2005). In populations with low inbreeding depression, selfing can provide reproductive assurance when pollinators are scarce (Eckert and Schaefer 1998; Fausto et al. 2001).

The main goal of this study was to study *S. lemmonii*'s pollination biology, which was relatively unknown previously. Invoking the concept of pollination syndromes, one would expect a night-blooming plant with pale petals such as *S. lemmonii* to be moth-pollinated (Proctor et al. 1996). Although *S. lemmonii* attracts noctuid moths during twilight and night hours, bees and flies visit flowers during daylight hours. Thus, a mixed pollination system (with both diurnal and nocturnal animals contributing to fruit set) appears to operate in the study population. Previous studies have also documented diurnal and nocturnal pollination of night-blooming plants (Barthnell and Knops 1997; Young 2002; Barthelmess et al. 2006; Dar et al. 2006; Saunders and Sipes 2006). In both years of this study, plants allowed access to daytime and evening pollination produced the most fruits and seeds.

An overall increase in fruit and seed set in 2000, the only year when I recorded noctuid moth visitation, suggests that these moths may be very efficient pollinators and that pollen limitation may occur in years when moths are absent. The fact that night-exposed plants exhibited greater fruit and seed set than their day-exposed counterparts in 2000 supports these hypotheses.

Visitor identity varied between years at the study site; this could be due in part to two factors. First, *S. lemmonii* flowers provide almost no nectar for pollinators (A. Hove, unpublished data). Therefore, nectar-foraging moths had little incentive to visit regularly and moth populations may not be well established at the site. Second, slight interannual differences in abiotic environmental parameters (such as temperature, soil moisture, or relative humidity) may help explain both differences in visitation rates between years and the absence of moths in 1999. While I did not regularly measure environmental variables, I also did not observe any dramatic differences in climate or the onset of flowering between the 1999 and 2000 flowering seasons. Additionally, in both years, I regularly observed insects foraging on other flowering plant species at the site.

Regardless of the differences in visitor identity observed between 1999 and 2000, diurnal and nocturnal insects only rarely visited flowers during those years. In 1999, the estimated visit

TABLE 6. COMPARISON OF MEAN FRUIT SET AND SEED SET OF PLANTS THAT WERE CAGED, PRUNED, EMASCULATED, OR UNMANIPULATED IN 2000. Pollen sources for each treatment are included in parentheses (*a* = autogamy, *i* = insect visitation, and *j* = jostling-induced geitonogamy). Means from the same year with different superscripts are significantly different (Fisher's LSD Multiple Comparison Test, *P* < 0.05). N = number of plants per treatment.

Treatment	Mean Fruit Set (SE)	N	Mean Seed Set (SE)	N
Caged (<i>a, j</i>)	0.10 (0.014) ^a	29	4.47 (0.57) ^a	20
Emasculated (<i>i</i>)	0.49 (0.039) ^b	31	10.36 (0.33) ^b	31
Pruned (<i>a, i</i>)	0.46 (0.064) ^b	22	14.82 (0.86) ^c	17
Unmanipulated (<i>a, i, j</i>)	0.61 (0.032) ^c	30	12.71 (0.24) ^d	30

number over a flower's lifetime (0.55 visits/flower) roughly corresponded to the average fruit set of open-pollinated plants (~40%). The estimated total of 0.55 insect visits per flower suggests that approximately one out of two flowers in the study population received a visit.

The low pooled visitation rate observed in 2000, which corresponds to an estimated 0.09 visit per flower over its lifetime, is more difficult to reconcile with that year's relatively high fruit set (~61%). One possible explanation for the discrepancy between fruit set and the pooled insect visitation rate is that insect visits occurred more frequently than observed, particularly at night when pairs of field workers used red lights to illuminate the plants. Although red lights have been used to observe visits to other *Silene* species (Pettersson 1991) as well as other moth-pollinated species (see Kearns and Inouye 1993), it is conceivable red lights may have repelled nocturnal visitors to *S. lemmonii*, leading to low calculated visitation rates for nocturnal insects.

Despite low insect visitation rates, fruit production at the study site appears to have been primarily insect-mediated in 2000. Almost half of the emasculated flowers set fruit, whereas ~61% of unmanipulated plants set fruit. The difference in fruit set between emasculated flowers (allowed only insect visits as a pollen source) and unmanipulated flowers suggests that insect pollination accounted for ~80% of fruit production of unmanipulated plants (Fig. 3). Other evidence suggests that the remaining 20% resulted from jostling-induced geitonogamy. Pruned plants had lower fruit set than unmanipulated plants (Table 6), indicating that jostling-induced geitonogamy aided in fruit production and/or that pruning inflorescences reduced insect visitation. Furthermore, fruit set of emasculated plants was about 12% lower than that of unmanipulated plants (Table 6), implying that jostling-induced geitonogamy contributed to the remaining ~20% of fruit production (Fig. 3).

Comparison of fruit set between the pruned and emasculated groups suggests that autonomous self-fertilization by autogamy did not occur. Flowers exposed to insect pollination and autogamy as potential pollen sources were as likely to set fruit as those solely dependent on insect visitors. Fruit set of caged plants was significantly less than fruit set in the other groups (Table 6), underscoring insect visitation as the most important component of pollination. Still, ~10% of the caged flowers developed into fruits, the result of either jostling-induced geitonogamy or autogamy. However, since flowers are strongly protandrous, I suspect that autogamy contributed minimally (if at all) to fruit set; fruit production by caged plants more likely resulted from jostling-induced geitonogamy.

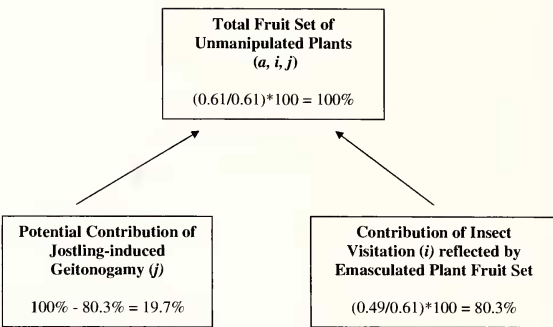


FIG. 3. Flowchart depicting the relative contribution of each source of pollen to total fruit set. If insect visitation (*i*) contributes ~80% and the probability of autogamy (*a*) is low, then jostling-induced geitonogamy (*j*) potentially contributes to ~20% of fruit set.

The results of this study provide evidence that jostling-induced geitonogamy contributes to fruit production in *S. lemmonii*. However, before fully accepting jostling-induced geitonogamy as a pollen transfer mechanism, three potential weaknesses in my experimental design must be addressed.

First, pruned plants may have been less attractive to foraging insects than unmanipulated plants. Reduced fruit set of pruned plants may have in turn resulted from fewer insect visits, rather than inflorescences' inability to jostle into one another. (Nonetheless, pruning plants was the most practical and feasible way to restrict jostling among inflorescences.) While some studies on other plant species have found that fruit set is not influenced by local plant density (Pettersson 1997; Bosch and Waser 1999; Somanathan et al. 2004), other studies (Brys et al. 2004; Somanathan et al. 2004) have clearly shown reduced fruit set in low-density plant populations. However, if pruned plants received fewer visits from insects attracted to large floral displays, then one would expect plants occurring in denser patches and displaying many flowers to have higher fruit set. A preliminary experiment I conducted in 1999 showed that neither local plant density nor the number of flowers per plant affected fruit and seed set in my study population. Though the density and pruning studies were not conducted simultaneously, the data imply that pruning plants had a minimal impact on their ability to attract insects.

Second, reduced fruit production by pruned plants is potentially attributable to two factors: the inability of flowers to jostle into one another and the injury inflicted upon plants by pruning inflorescences. I attempted to minimize plant injury by only clipping inflorescence rachises and leaving foliage leaves and vegetative stems untouched. However, future research on jostling-induced geitonogamy in *S. lemmonii* would benefit from developing a method to spatially

separate inflorescences without pruning them. Interestingly pruned plants produced more seeds than plants from the other three treatment groups (Table 6), possibly because with fewer flowers pruned plants could allocate more resources to each fruit for seed production. Other studies have also shown increases in reproductive output following the partial loss of plant parts (Mabry and Wayne 1997; Fang et al. 2006).

Third, lower fruit set of emasculated plants in comparison to unmanipulated ones could be attributed to fewer visits by pollen-foraging insects. However, these plants were, with the exception of bare stamens, similar in floral display to unmanipulated ones. Moreover, syrphid flies, presumably foraging on pollen, landed on female-phase flowers, even when withered stamens displayed no fresh pollen (A. Hove, *personal observation*).

Although insect pollination and jostling-induced geitonogamy evidently contributed to fruit set in 2000, the possibility of wind pollination should also be considered. Goodwillie's (1999) study of *Linanthus parviflorus* showed that wind pollination provides reproductive assurance when insect visitation is low. However, her study site was a relatively open area, consisting of oak woodlands and grasslands. Wind pollination of other entomophilous species growing in windy, exposed areas has also been recorded (Gómez and Zamora 1996; Norman et al. 1997; Lazaro and Traveset 2005). Because the forest understory surrounding Dubakella Mountain is sheltered from wind, long-distance travel by pollen grains on wind currents does not seem likely. However, a future study involving the placement of pollen traps next to flowers throughout the population using methods similar to Goodwillie's (1999) is necessary to rule out the possibility of wind pollination in *S. lemmonii*.

Although no previous studies have documented it, jostling-induced geitonogamy probably occurs in other self-compatible plant species. This type of self-pollination seems especially likely to operate in plant species that produce several inflorescences bearing pendant flowers with exerted reproductive structures. Jostling-induced geitonogamy may also serve as an additional pollination source for species where autogamy is unlikely to occur because flowers separate pollen presentation from stigma receptivity either spatially (herkogamy) or temporally (dichogamy).

In summary, the majority of fruit production resulted from diurnal and nocturnal insect pollination in my study population, yet jostling-induced geitonogamy likely contributed to fruit set. Recent work has shown that mixed mating systems, wherein individuals reproduce via a combination of selfing and outcrossing, may be more common than previously thought (Goodwillie et al. 2005); besides *S. lemmonii*, mixed mating also

occurs in multiple *Silene* species (Kephart et al. 1999; Davis and Delph 2005; Keller and Schwaegerle 2006). However, at the study site *S. lemmonii* appears to self-pollinate by jostling-induced geitonogamy rather than autogamy. Yet, it seems unlikely that jostling-induced geitonogamy has evolved as a mechanism to promote reproductive assurance in *S. lemmonii*. A more likely explanation lies in the fact that the glandular inflorescence trichomes that facilitate floral jostling serve primarily to protect plants from crawling herbivores. Trichomes are a well-known herbivore defense mechanism (Hare and Elle 2004; Handley et al. 2005). Instead of a mating system adaptation, selfing via floral jostling may be an incidental process that can persist in populations where inbreeding depression is low enough for the defensive benefits of glandular inflorescence trichomes to outweigh any costs associated with selfing. However further empirical work examining the potential role of herbivory in the maintenance of mixed mating in multiple *S. lemmonii* populations is needed to confirm this hypothesis.

In the population I studied, inbreeding depression does not appear to limit self-fertilization. Self-pollinated flowers produced seeds and fruits as well as outcrossed ones during the years of this study. However, to fully understand the potential effect of inbreeding, future studies should examine the genetic structure of *S. lemmonii* populations and compare selfing rates as well as fitness among populations from various locations in this species' geographic range. Comparing the progeny of selfing and outcrossing plants using other measures of fitness, such as seedling survival and seedling vigor, will also provide greater insights regarding the implications of mixed mating in this species.

ACKNOWLEDGMENTS

Michael Mesler was an invaluable source of support and insight throughout this project. Scott Hove, Alex Yelich, Laura Julian, and Sylvie Thome cheerfully and diligently helped with much of the field work. Special thanks go to Scott Hove, Allyson Carroll, Ben Fitzpatrick, Erik Jules, and Michael Mesler for providing comments on previous drafts of this manuscript. Bill Rice shared helpful comments regarding statistical analyses. Additional comments by Susan Kephart and one anonymous reviewer also greatly enhanced the quality of this manuscript. The Humboldt State University Department of Biological Sciences, the Eureka Rotary Club, and the Mazamas provided funding for this project.

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